XYLEM MONOTERPENES OF PINUS PONDEROSA, P. WASHOENSIS, AND P. JEFFREYI IN THE WARNER MOUNTAINS OF CALIFORNIA

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In the Warner Mountains of northeastern California, the subsection Ponderosae of the genus *Pinus* is represented by three species: ponderosa pine (*Pinus ponderosa* Laws.), Washoe pine (*P. washoensis* Mason & Stockwell), and Jeffrey pine (*P. jeffreyi* Grev. & Balf.). Washoe was initially reported to be confined to a small stand at Patterson Meadow at the Warners' southern end (Haller, 1961), but it will probably be greatly enlarged by more recent studies. Ponderosa is found quite extensively throughout the area. Jeffrey grows considerably less extensively than ponderosa but much more extensively than Washoe, though limited to the southern end of the Warners (Critchfield and Little, 1966). Botanically, the area is of interest because it lies on the northeastern fringe of the range of Jeffrey pine and contains one of the isolated stands of Washoe.

The monoterpene composition of the xylem resin of ponderosa is extremely variable, while that of the other pines is much less variable and can be somewhat stereotyped (Mirov, 1961; Smith, 1964; 1967). The composition of an average ponderosa pine from low elevation in the Warners is about 7% α-pinene, 25% β-pinene, 46% 3-carene, 10% myrcene, 9% limonene, 1% β-phellandrene, and 2% terpinolene. A normalized composition for average Washoe is 5% α-pinene, 10% β-pinene, 65% 3-carene, 15% myrcene, 1% limonene, 1% β-phellandrene, and 3% terpinolene and some trace components; Jeffrey pine is about 95% heptane, 2% nonane, and the remaining 3% divided among several of the monoterpenes.

Individual ponderosa pines have been found whose monoterpene composition falls within the average composition of Washoe. A few such trees have been found in low-elevation stands in the northern Warners and in stands in the central and northern Rocky Mountains. These ponderosa stands in the eastern portion of its range often are classified as *P. ponderosa* var. *scopulorum* Englem.

In 1965–66 a study was made of the monoterpene composition of the xylem resin of ponderosa or Washoe or both in three areas of the Warner Mountains (fig. 1) to determine a, range of stands which could be classified as Washoe on the basis of monoterpene composition, b, how often individual trees in ponderosa stands showed the full characteristics of Washoe monoterpenes, and c, the possibility of hybridization among the three species. Jeffrey pine was studied in the southern area where it grows with ponderosa or Washoe or both.

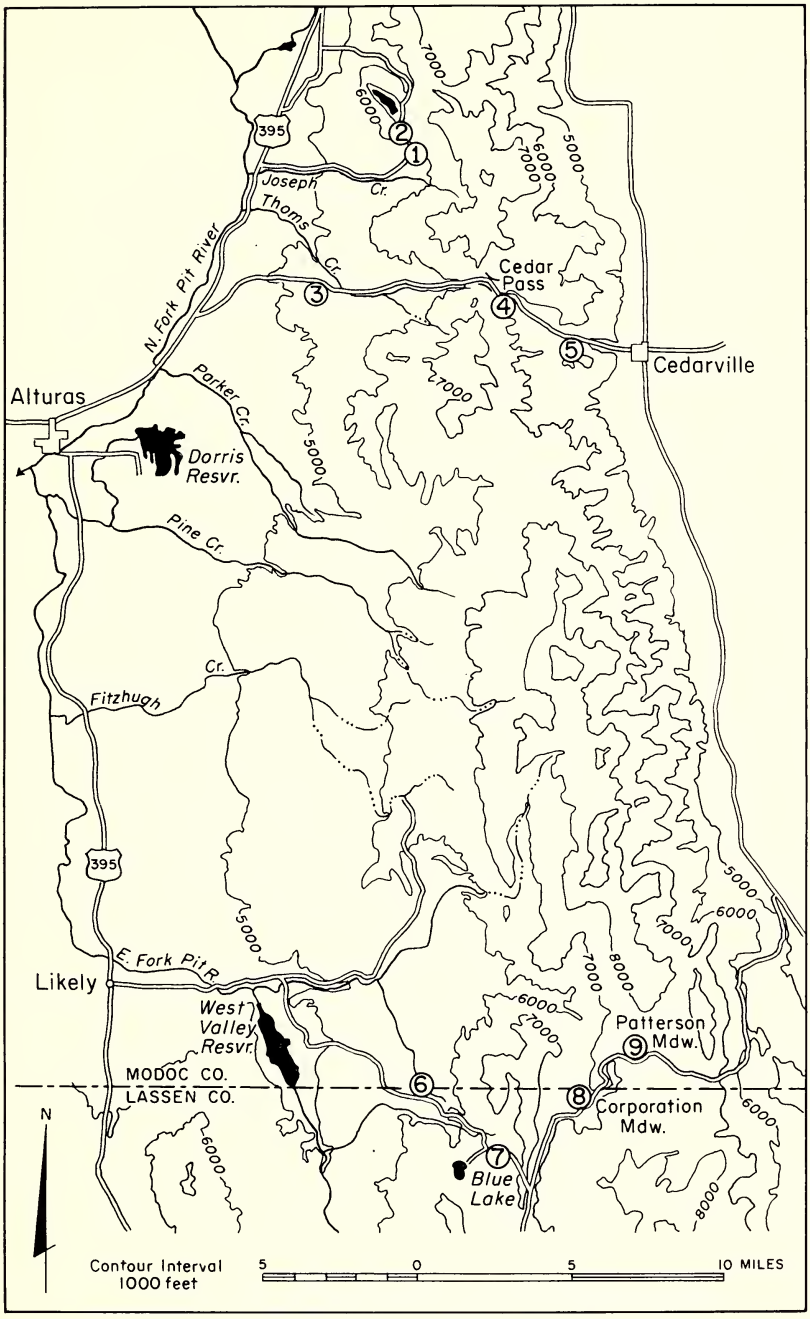

FIG. 1. Location of study plots (0) and their elevation in three areas near Alturas, Modoc Co., Calif.

Table 1. Individual Trees Selected From Each Plot to Show Characteristic Major Monoterpene Composition of Washoe Pine in Percent

Plot No.	α-pinene	β-pinene	3-carene	Myrcene	Limonene
1	7	1	69	17	Trace
	6	1	65	22	1
2	6	20	60	8	Trace
	6	14	62	12	1
3	7	4	69	13	1
	15	14	60	6	Trace
4	3	16	63	11	1
5	4	1	79	10	Trace
	10	2	74	8	Trace
	16	1	68	10	Trace
6	8	4	66	15	Trace
	3	6	71	15	Trace
	7	4	69	12	2
7	4	1	78	12	1
	6	3	69	15	Trace
	6	4	65	19	Trace
8	5	11	64	14	Trace
	6	8	65	16	Trace
	6	12	60	17	1
9	5	4	73	12	1
	5	2	78	9	—
	9	1	65	19	Trace

Two to four plots were selected at different elevations in the three areas. The elevation at each plot is as follows: plot 1, 5,500 ft.; plot 2, 5,700 ft.; plot 3, 5,000 ft.; plot 4, 6,000 ft.; plot 5, 5,000 ft.; plot 6, 5,800 ft.; plot 7, 7,000 ft.; plot 8, 6,800 ft.; and plot 9, 7,200 ft. About 20 trees per plot were tapped for resin at plots 1 to 8, inclusive. Except for the Jeffrey pines, no effort was made to describe the trees morphologically; they were selected simply on the basis of geography. Previous data gathered for the Patterson Meadow location of Washoe were included for a reference as the ninth plot.

I used previously described procedures for tapping the trees, preparing the samples for analysis, and analyzing the samples by gas chromatography (Smith, 1964). All results of analysis are based on the normalization of the monoterpene fraction of the xylem resin; i.e., each monoterpene is expressed as a percent of the total monoterpenes.

Results

The frequency distribution of each of the five major components—α-pinene, β-pinene, 3-carene, myrcene, and limonene—in each of the nine plots is given in figure 2. Trees with the typical composition of Washoe pine were found in each location (table 1). The frequency of this type of tree seemed to shift markedly between 6,000 and 7,000 feet; plots below this zone (plots 1–6) can be classified as typical ponderosa stands, containing a scattering of trees which have monoterpene char-

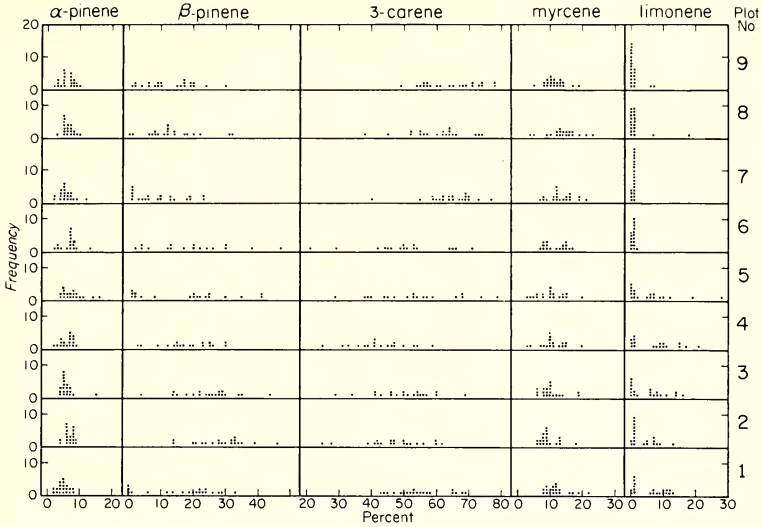

FIG. 2. Frequency distribution of the five major monoterpenes of Washoe and ponderosa pine from nine plots in the Warner Mountains, northeastern California.

acteristics of Washoe, comprising generally about 10% of the stand. Trees at higher elevation are typical Washoe; in these plots (7–9) an infrequent tree has the monoterpene characteristics of ponderosa pine, comprising generally about 10% of the stand. In addition to trees in low-elevation stands with all the monoterpene characteristics of Washoe, individual trees may be found which show at least one of the characteristics of Washoe; i.e., either $>$ 60% 3-carene, $<$ 20% β-pinene, or $<$ 2% limonene. The occurence of these two types of trees suggests the possibility of both geographical and physiological mixing of ponderosa and Washoe.

This study also suggested that the previously defined range of Washoe in this area should be enlarged (Haller, 1961). If a criterion of $>$ 60% 3-carene, $<$ 20% β-pinene, and $<$ 2% limonene is used for Washoe pine, 10% of the trees below the 6,000- to 7,000-foot zone fit this criterion and might be called Washoe; 38% of the trees above this zone do not fit this criterion and might be called either ponderosa or hybrids between ponderosa and Washoe. There is some evidence that plot 6, at about 5,800 feet, is near the transition zone, since the frequency distribution of limonene for the trees in this plot (fig. 1) is typical of Washoe, while the 3-carene and β-pinene distributions are typical of ponderosa.

Limonene was of particular interest in this study. Except in a few instances it is lacking in trees from the typical Washoe plots; in all plots considered typically ponderosa in the Warners or the Sierra Nevada it may be absent or it may occur in an amount of from about 5 to 10%.

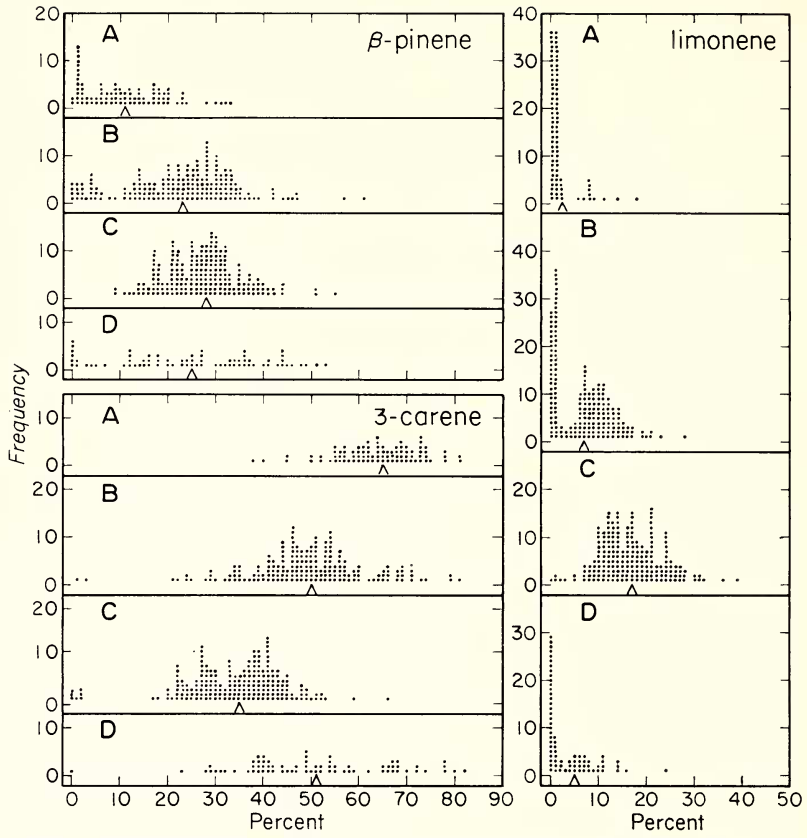

FIG. 3. Frequency distribution of β-pinene, limonene, and 3-carene from four sources: A, Washoe pine, B, low-elevation ponderosa in Warner Mts., C, ponderosa from central Sierra Nevada, D, var. *scopulorum* of ponderosa from Colorado. Wyoming, and Nebraska.

Only a few trees had between 1 and 5%.

The Jeffrey pines growing at plot 6 were found to be very similar to those in the Sierra Nevada, but the group included one tree that had a monoterpene composition highly suggestive of that of a hybrid between Jeffrey and Washoe. Its composition was 17% heptane, 2% nonane, 2% α-pinene, a trace of α-thujene, 4% β-pinene, 55% 3-carene, 6% myrcene, 11% limonene, and 3% terpinolene. The amounts of heptane and nonane are clear signs of Jeffrey pine. The low β-pinene, high 3-carene, and trace of α-thujene are the basis for believing the other parent is Washoe. However, the 11% limonene suggests that ponderosa could be the other parent. There is always the rather remote possibility of a three-way hybrid.

Hybrids have been artificially produced between Jeffrey and both ponderosa and Washoe (Liddicoet and Righter, 1960) but not without

Table 2. Differences Among Means of Limonene and t-Values of Four Sources of Ponderosa or Washoe Pine

Comparison	$X_1 - X_2$	d.f.	t
Washoe vs. Warner, low elevation	5.2	272	5.10**
Washoe vs. Sierra Nevada	16.1	290	7.02**
Washoe vs. var. *scopulorum*	2.8	158	2.01*
Warner, low elevation vs. Sierra Nevada	10.9	388	4.52**
Warner, low elevation vs. var. *scopulorum*	2.4	258	2.88**
Sierra Nevada vs. var. *scopulorum*	12.3	274	5.20**

*= 95, and ** = 99% level of confidence for rejecting the null hypothesis.

difficulty (Critchfield and Little, 1966). Natural hybrids between Jeffrey and ponderosa have been found (Mirov, 1929), but natural hybrids between Jeffrey and Washoe have not been reported. The Jeffrey pines in the Warners are growing in a stand which chemically might be called ponderosa with a scattering of Washoe.

A frequency distribution of limonene, β-pinene, and 3-carene was made of four sources of ponderosa or Washoe pine (fig. 3): 1, typical Washoe sources (plots 7–9 plus data from Smith (1967)); 2, ponderosa at low elevations in the Warner Mountains (plots 1–6 plus previous data gathered near plot 1); 3, ponderosa from the central Sierra Nevada (Smith, 1966); and 4, ponderosa from Wyoming, Colorado, and Nebraska, where it is usually called var. *scopulorum* (Peloquin, 1964). This last grouping is a collection of trees from widely separate locations; but they do represent the whole region fairly well.

A null hypothesis was established that there was no difference in the limonene percentage among the various sources; a t-test of arc-sin transformed percentages shows that this null hypothesis can be rejected at the 95% or greater level of confidence in all comparisons among the four sources (table 2). However, from a visual inspection of the frequency distribution, it does appear that low-elevation ponderosa in the Warners is somewhat intermediate between central Sierra Nevada ponderosa and var. *scopulorum* but may be more closely related to var. *scopulorum*.

Conclusions

This study of xylem monoterpenes suggests: 1, that the range of Washoe pine in the southern Warner Mountains should be enlarged; 2, that some ponderosa stands have geographically mixed with Washoe stands; 3, that composition of the monoterpenes of the two species may overlap considerably; 4, that the two species hybridize naturally; 5, that Washoe is closely related to ponderosa, particularly to var. *scopulorum;* and 6, that low-elevation ponderosa in the Warners is intermediate between Washoe pine and ponderosa pine of the central Sierra Nevada of California.

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STUDIEDS IN THE RHODOPHYLLOID FUNGI. I. GENERIC CONCEPTS

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This paper is concerned with the Rhodophyllaceae in the sense of Singer (except *Clitopilus* and *Rhodocybe*).

In 1821 Elias Fries classified the rhodophylloid fungi into tribes which were distinguished by variations of the following features: 1, consistency of the carpophore, particularly of the stipe, 2, attachment of the lamellae, 3, shape of the pileus, and 4, nature of the pileal surface. In 1838 he further emphasized the nature of the pileal surface as a diagnostic feature, using it as well as other characteristics to divide the tribe *Entoloma* into three sections, and admitted species with flocculose pilei to tribe *Nolanea,* which previously had contained only mushrooms with glabrous pilei. In subsequent publications Fries no longer used the pileal surface in diagnostic characterizations but defined his tribes (which he now called subgenera) only on the basis of consistency of stipe, type of pileal margin, and attachment of lamellae. These three features have continued to be used by mycologists who have chosen to maintain the Friesian groupings, whether at the generic or subgeneric level. Unfortunately all three are variable, or hard to assess, or both. The difficulty of accurately defining taxa by such features has led some